

SEED PRODUCTION IN *GENTIANA NEWBERRYI* (GENTIANACEAE)

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ABSTRACT.—Experimental manipulations and observations in one population of *Gentiana newberryi* Gray flowers over 2 years showed significant variation in seed production relative to pollinator and soil water availability. When pollinators were rare, there was a significant relationship between number of bees present and number of mature seeds produced, and supplemental hand cross-pollination (xenogamy) did improve seed set in *Gentiana newberryi* Gray. When pollinators were abundant, supplemental hand cross-pollination did not increase seed set. Self-fertilized seeds (autogamy) germinated at the same rate as cross-pollinated seeds. Seed production in unvisited flowers is probably limited anatomically and is not influenced by the type of fertilization. There was a significant relationship between soil moisture and flower size in *G. newberryi*, with larger flowers found in wetter areas.

Key words: *Gentiana*, seed production, pollination, bumblebees, soil water potential.

Seed set can be limited by insufficient pollinator visits (Levin and Anderson 1970, Thomson 1980, 1981, Bierzychudek 1981, Gross and Werner 1983, Pleasants 1983, Waser 1983a, Motten 1986, Galen and Newport 1988, Calvo and Horvitz 1990, Harder 1990, Ashman and Stanton 1991) or by other resources, such as water or nutrients, in populations with sufficient pollinators (Stephenson 1981, Evenson 1983, McDade and Davidar 1984, Primack and Kang 1989). Resource limitation may result in aborting the whole fruit or only some seeds in a fruit (Lee 1988). Multiple reproductive strategies in perennials, including cross-pollination, self-compatibility (Levin 1971, Jain 1976, Barrett 1988, Karoly 1992), and vegetative reproduction (Evenson 1983, Waller 1988), are advantageous in populations where pollinators and other resources are unpredictable (Motten 1982, Sutherland 1986, Ehrlen 1992). While self-fertilized and vegetatively produced plants increase the risk of inbreeding depression, those that are successful may have coadapted genes that are advantageous for current environmental stresses (Lloyd 1979, Waser and Price 1982, Barrett 1988).

Optimal flowering time is when a plant can attract the most visitors and still be able to set seed during the growing season (Pleasants 1983, Waser 1983b, Primack 1987). When bees are abundant, pollination does not limit seed set. When bees are infrequent, there is often a correlation between seed set and polli-

nator visitation rate (Zimmerman 1980, McDade and Davidar 1984, Zimmerman and Pyke 1988). Supplemental hand pollination can be used to determine whether pollinators or climatic factors are limiting seed set (Motten 1983).

Here we present both observational and experimental data on seed production in *Gentiana newberryi* Gray. These perennial plants are restricted to high-elevation wet meadows in eastern California, western Nevada, and southern Oregon (Munz 1973). *Gentiana newberryi* has protandrous, funnel-shaped flowers that are usually white with greenish spots (Munz 1973). Each ramet has one or two flowering shoots with one or two terminal flowers (personal observation). They can reproduce sexually and vegetatively (Spira 1983, Spira and Pollak 1986).

Initial observational data included pollination mode, pollinator activity, and soil moisture effects on seed production. Based on observational information, we then measured soil water potential and pollinator visitation across the study area and throughout the season to determine relationships between pollinator availability or soil moisture and seed production.

METHODS AND MATERIALS

Study Site

In August 1991 we selected a 2700-m² study site at Little Valley, 27.3 km southeast of

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Reno, Nevada (119°52'W, 39°15'N). The site, located at an elevation of 2000 m along the eastern edge of the Sierra Nevada escarpment, is part of the 1200-ha Whittell Forest and Wildlife Area owned by the University of Nevada, Reno (Rust 1987). The area is covered by snow each winter but has an average of 120 days with minimum temperatures above 0°C (Houghton et al. 1975). *Gentiana neuberryi* populations are found in meadows that collect and retain snowmelt water longer than surrounding meadow areas. A small creek running through the southern portion of the site keeps the areas near the creek wet throughout the growing season. Central and northern portions of the site dry out toward the end of the growing season. The study was conducted during the fifth and sixth years of a drought when snowfall was only 50% of normal (James 1992). Most flower species began flowering 4 weeks earlier than usual in 1992 (personal observation) after a warm spring and early snowmelt (James 1992).

Population Characteristics

In mid-September 1991 and 1992, numbers of plants (ramets) and flowers on the study site were estimated using 11 transects (38–54 m long) placed 5 m apart and extending across the population to include all *G. neuberryi* plants. At each meter along each transect all plants and flowers were counted and percentage of *G. neuberryi* coverage was estimated within 0.5-m² circular quadrats.

Floral Characteristics

In 1992, after observing the differential drying of the study site in 1991, we divided the site into five areas. Area 1 was adjacent to the southern creek (always wet during 1991). Areas 2 to 5 were equally spaced away from the creek, with area 2 the closest to area 1 and area 5 the farthest removed. Soil water potential was measured in each area weekly with a Quickdraw Series 2900 Soil Moisture Probe. Moisture was measured at approximately 30 cm. Three measurements were taken per area per week. Petal length and maximum corolla tube width were measured for 10 random *G. neuberryi* flowers (each from a different plant, and with dehiscing anthers) in each area in 1992 ($n = 50$). An index was developed to compare flower size by multiplying petal

length by corolla tube width. Ultraviolet reflectiveness was determined by photographing numerous buds and open flowers on live plants in the field with a Wratten 18A UV filter.

On 21 August 1991, 10 mature bud flowers (ready to open) were marked and covered with waxed paper bags (1 in the wet area and 9 in the dry). Another 13 buds were marked and left uncovered (7 in the wet and 6 in the dry area). At 0900 the following morning, nectar volume in each flower was measured using a 1- μ l capillary tube. On 13 September 1991, 10 mature bud flowers in the dry area and 13 in the wet area were bagged. The following afternoon (1300) nectar was measured from each flower. Each week during 1992 nectar was measured at approximately 0900 from one randomly selected, uncovered, dehiscing flower in each of the five soil moisture areas ($n = 60$).

Pollinators

Bumblebees were common throughout August and September 1991, but the number of bees present was not regularly recorded. Individual foraging bees were followed; and the flowers visited, distance between flowers, and times were recorded. In 1992 a 100-m transect was established across the drier part of the site and a 50-m (shorter due to limits of the wet area) transect placed across the wet area. These transects were walked hourly at least 2 days each week, and any bees observed within 5 m of the transect were recorded. A sample of all insect visitors to *G. neuberryi* was collected for identification by R. Rust, University of Nevada, Reno, and R. Brooks, University of Kansas, Lawrence.

Seed Production

In 1991 flower buds of *G. neuberryi* were randomly selected with not more than one flower per plant and marked with numbered paper tags ($n = 113$). Three times each week the phenology (bud, flower opening, dehiscing anthers, receptive stigma, and seed capsule formation) of each marked flower and soil moisture conditions adjacent to the plant (visually) were recorded. During 1992 two newly opened flowers on different plants with dehiscing anthers in each area were randomly selected and marked each week from early July through early October ($n = 84$). Mature seed capsules for all marked flowers were collected

and placed in individual waxed paper bags. Mature seeds and undeveloped ovules were counted using a dissecting microscope. Seeds for each flower with any mature seeds were placed in individual waxed paper bags and stored outdoors in Reno, Nevada.

During August 1991, 53 *G. newberryi* buds were randomly selected and marked, and the plants covered with white nylon organdy (100-mesh) bags over wire frames. When the flowers opened, 9 were hand-pollinated using a paint brush bearing pollen from a flower on the same plant (geitonogamy), 12 with pollen from a different plant (xenogamy), and 34 were left to self-pollinate (autogamy). During the week of 18 August 1992, 10 plants (2 in each soil moisture area) with bud flowers were selected at random, marked, covered with nylon organdy bags, and allowed to self-pollinate. Ten other newly opened flowers in the different areas were marked and cross-pollinated by hand after the stigma became receptive. Another 10 flowers in the different areas were marked and left alone for natural pollination. Mature seed capsules for treatments used in 1991 and 1992 were collected and seeds counted and stored using the same method.

Each year five randomly chosen seed capsules from each treatment and the open flowers were germinated. Seeds for each flower were placed in a petri dish on brown paper over kimpack moistened with a 400 ppm gibberellic acid solution. Seeds were kept at 15°C for 7 d and then alternated between 15°C for 12 h and 25°C for 12 h for 7 d in the dark.

Statistical Analyses

Analysis of variance (GLM in SAS 1990) was used for all comparative analyses between years and between areas or weeks within each year. Bonferroni *t* tests were used for multiple comparisons when analysis of variance indicated a significant difference. Arcsine transformations were used for analysis of percentage data (Zar 1974). Linear regression (SAS 1990) was used to determine if there was a relationship between soil moisture and flower size, soil moisture and seed production, or seed production and bee visits each week. Plant distribution was determined using the standardized Morisita index (I_p ; Krebs 1989).

RESULTS

Population Characteristics

There was no significant difference between 1991 and 1992 in number of plants ($F = 0.43$, $df = 1,984$, $P = .51$) or number of flowers ($F = 1.16$, $df = 1,984$, $P = .28$) per quadrat (Table 1). Percentage cover was significantly different between years ($F = 3.97$, $df = 1,984$, $P = .04$) (Table 1). Distribution of plants is clumped throughout the study site as indicated by the Morisita index ($I_p = 0.51$).

Floral Characteristics

A significant difference in *G. newberryi* flower size (petal length \times maximum corolla tube width) was found among the five soil moisture areas of the study site in 1992 ($F = 37.04$, $df = 4,45$, $P < .0001$; Table 2). There was a significant regression ($y = 693.4 + 12.5x$) between soil water potential and flower size ($F = 117.79$, $df = 1,48$, $P < .0001$; $R^2 = .71$), with larger flowers found in wetter areas.

Ultraviolet images of *G. newberryi* flowers show a dark, central, UV-absorbing bullseye pattern in the corolla tube and a dark longitudinal stripe on the outside of each petal from the base to the apex. Outer petal stripes are also visible on flower buds.

In 1991, in a sample of newly opened flowers at 0900 h, there was no difference in the amount of nectar available between flowers covered with a bag overnight (0.1 ± 0.1 [mean and standard deviation], range 0–0.3 μ l) and those left open (0.1 ± 0.1 , range 0–0.3 μ l) ($F = 0.03$, $df = 1,22$, $P = .97$) or in the amount of nectar in flowers between wet area (0.4 ± 0.4 , range 0–1.4 μ l) and dry area (0.2 ± 0.2 , range 0–0.7 μ l) ($F = 2.02$, $df = 1,21$, $P = .17$). In 1992 there was no difference in the amount of nectar available in open flowers between

TABLE 1. Number of *G. newberryi* plants, flowers, and percentage of cover per 0.5-m² quadrat at Little Valley, Nevada. Values are means \pm standard deviation; $n = 493$. Total numbers of plants and flowers in 2700-m² study site are in parentheses.

Plants (no.)	Flowers (no.)	Percent cover
----- 1991 -----		
1.2 \pm 3.7 (3115)	2.3 \pm 3.1 (773)	1.7 \pm 5.5
----- 1992 -----		
1.1 \pm 4.1 (2710)	0.2 \pm 1.1 (476)	1.1 \pm 5.4

TABLE 2. Relationship between soil water potential and flower size in *G. newberryi* at Little Valley, Nevada, in the second week of July 1992. Soil water potential, petal length, corolla width, and a flower size index (petal length \times corolla width) are indicated for five areas of decreasing soil water potential. Values are means \pm standard deviation; $n=10$.

Area	Soil water potential (MPa)	Petal length (mm)	Corolla width (mm)	Flower size index	
1	0.0 \pm 0.0	46.5 \pm 2.4	16.4 \pm 1.0	764.1 \pm 79.0	A ^a
2	-3.5 \pm 0.5	44.0 \pm 3.5	14.0 \pm 1.8	617.6 \pm 106.8	B
3	-6.0 \pm 1.6	41.7 \pm 3.6	13.3 \pm 1.9	557.7 \pm 105.5	B
4	-12.0 \pm 4.9	38.3 \pm 3.1	11.0 \pm 1.9	425.1 \pm 102.3	C
5	-35.0 \pm 0.0	33.1 \pm 2.9	8.6 \pm 1.8	287.5 \pm 74.4	D

^a Bonferroni *t* tests comparing differences in flower size index among areas. Means with the same letter are not significantly different ($P < .05$).

weeks (week 1—0.1 \pm 0.1, range 0–0.3 μ l; week 2—0.6 \pm 0.9, range 0–2.1 μ l; week 3—0.4 \pm 0.3, range 0–0.7 μ l; week 4—0; week 5—0.7 \pm 0.4, range 0.4–1.3 μ l; week 6—0.1 \pm 0.2, range 0–0.4 μ l; and week 7—0.2 \pm 0.2, range 0–0.4 μ l) ($F = 1.99$, $df = 6,28$, $P = .10$). No difference in amount of nectar was found between areas (area 1 [driest]—0.1 \pm 0.2, range 0–0.5 μ l; area 2—0.3 \pm 0.2, range 0–0.6 μ l; area 3—0.2 \pm 0.3, range 0–0.7 μ l; area 4—0.4 \pm 0.4, range 0–1.3 μ l; and area 5 [wettest]—0.6 \pm 0.8, range 0–2.2 μ l) ($F = 1.01$, $df = 4,30$, $P = .41$). Most nectar was usually found in one or two of the five nectar tubes.

Pollinators

In 1991 four species of bumblebees were observed visiting *G. newberryi* flowers (Table 3). Most visits were for nectar. Nectar foragers would pick up pollen on their ventral surface from the centrally located anthers. *Bombus appositus* Cresson and *Bombus edwardsii* Cresson were frequent visitors to *G. newberryi* from early August until the end of September. *Bombus vosnesenskii* Radoszkowski was frequently observed visiting *Lupinus sellulus* Kell. adjacent to *G. newberryi* and occasionally visited a few *G. newberryi* flowers. *Bombus ferridus* (Fabricius) was seen visiting *G. newberryi* flowers during only one week in August. Usually between one and six bumblebees could be found visiting *G. newberryi* flowers on the study site anytime during August and September when the weather was warm and calm.

During 1992, bumblebee visits to *G. newberryi* were rarely observed. A few visits by

Bombus edwardsii were seen. *Bombus vosnesenskii* were observed visiting other flower species and occasionally robbed nectar from *G. newberryi* from outside the flower. *Anthophora bombooides* Kirby, *A. urbana* Cresson, and *A. terminalis* Cresson were occasionally observed visiting *G. newberryi*. *Apis mellifera* L. were common visitors to adjacent *Lupinus sellulus*, and one was seen visiting a *G. newberryi* flower. *Anthophora* species and *A. mellifera* were not seen in 1991.

In 1992 there were always many flowers open with pollen available. Less than one bee per 750 m² was observed when walking transects. There was a significant positive correlation between number of bees observed each week along the combined transects and number of seeds produced per flower marked that week (Fig. 1).

Seed Production

There was no significant difference in the mean number of mature *G. newberryi* seeds produced per marked flower between 1991 (116.2 \pm 143.6, $n = 58$) and 1992 (135.4 \pm 114.4, $n = 76$) ($F = 0.75$, $df = 1,132$, $P = .38$). When we eliminated flowers with aborted seed capsules from the analysis (50% aborted 1991, 23% 1992), the number of mature seeds per capsule was higher in 1991 (232.4 \pm 118.3, $n = 29$) than 1992 (174.6 \pm 100.0, $n = 59$) ($F = 5.76$, $df = 1,86$, $P = .01$).

In 1991 significantly more seeds were produced by *G. newberryi* flowers in the areas with a wet soil surface (210.3 \pm 175.1, $n = 20$) than in the dry areas (66.7 \pm 93.4, $n = 38$) ($F = 16.70$, $df = 1,56$, $P < .0001$). More seed capsules aborted in the dry than the wet area

TABLE 3. Total number of visits, mean length of visits, and mean distance traveled between flowers for varying numbers of individuals of four foraging *Bombus* species at Little Valley, Nevada, in August 1991. Values for time and distance are mean \pm standard deviation.

Species	Individuals	Visits	Time (sec)	Distance (cm)
<i>B. appositus</i>	1	6	10.3 \pm 0.7	13.5 \pm 8.3
<i>B. edwardsii</i>	1	20	12.8 \pm 4.5	9.1 \pm 24.7
<i>B. ferridus</i>	5	45	14.7 \pm 9.2	64.4 \pm 98.2
<i>B. rosnesenskii</i>	3	26	8.2 \pm 5.6	23.5 \pm 23.2

(58% vs. 35%). A higher percentage of ovules per capsule matured to seed in the wet area (84.7 \pm 10.8%, $n = 13$) than in the dry area (60.2 \pm 24.0%, $n = 16$) ($F = 5.88$, $df = 1,27$, $P = .01$).

In 1992 there was no significant difference in the number of mature seeds produced per flower between the areas with varying soil water (area 1 [driest]—133.7 \pm 112.5, area 2—153.1 \pm 98.4, area 3—57.0 \pm 79.3, area 4—161.9 \pm 135.8, and area 5 [wettest]—142.1 \pm 122.8) ($F = 2.26$, $df = 4,79$, $P = .07$) or in the percentage of ovules that matured to seed per capsule ($F = 0.56$, $df = 4,60$, $P = .69$). There was, however, a significant positive relationship between soil water at the time a flower opened and number of mature seeds produced ($y = 158.9 - 2.3x$ and $F = 5.96$, $df = 1,69$, $P = .02$).

There was a significant difference in the average number of seeds produced ($F = 8.44$, $df = 3,83$, $P < .0001$) and the percentage of ovules that matured to seeds ($F = 9.06$, $df = 3,42$, $P < .0001$) between the open, xenogamous, and geitonogamous versus autogamous pollination treatments in 1991 (Table 4). In 1992 there was also a significant difference between pollination treatments of open and xenogamous versus autogamous in the average number of seeds produced ($F = 11.37$, $df = 2,20$, $P = .0005$) and the percentage of mature seeds per capsule ($F = 8.15$, $df = 2,25$, $P = .002$) (Table 4). Hand cross-pollinated (xenogamy) seed production was highest but was not statistically different from open bee pollination in both years. Autogamous seed production was lowest but not statistically different from open pollination.

The percentage of germinated *G. newberryi* seeds was not significantly different

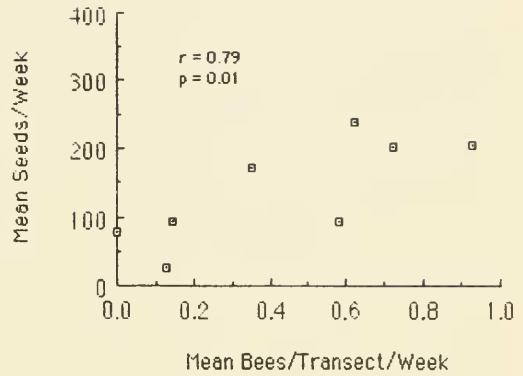


Fig. 1. Correlation between mean number of bees observed along combined transects and mean number of seeds produced by *G. newberryi* flowers that were open the week bees were observed; $n = 7$.

between treatments in 1991 ($F = 2.00$, $df = 3,15$, $P = .15$) or 1992 ($F = 2.93$, $df = 2,9$, $P = .10$). Seed germination ranged from 91.5 to 98% in 1991 and 84.8 to 98.8% in 1992 for all treatments.

DISCUSSION

Seed production per marked *Gentiana newberryi* flower was not significantly different between 1991 and 1992 in Little Valley, even though pollinator numbers and soil moisture were different between the 2 years. The large variation observed in all measurements of *G. newberryi* population characters and flower/seed characters in the Little Valley population both among and between years suggests much individual variability. Within the *G. newberryi* habitat area, individuals respond to a variety of localized microenvironmental parameters with the resulting variation in sexual reproductive output.

Bumblebees visiting *G. newberryi* were abundant during 1991. It is unlikely that pollinators limited seed set in 1991 since flowers with hand cross-pollination did not set significantly more seeds. There was a higher number of aborted fruits in the dry area in 1991. During 1992, when soil was wetter, *G. newberryi* plants appeared more vigorous throughout the study area. Low pollinator availability in 1992 did appear to limit seed set, as the number of flowers that matured seeds each week was correlated to the number of bees observed. Zimmerman (1980) and McDade and Davidar (1984) both found that seed set was correlated with visitation rates when pollinator numbers

TABLE 4. Percentage of mature seeds per capsule and number of mature seeds per flower in four pollination treatments. Treatment 1 = open, 2 = hand cross-pollinated, 3 = self-pollinated, 4 = hand-pollinated from flower on same plant. Aborted seed capsules were not included in the percentage of mature seeds per capsule analysis. Values are mean \pm standard deviation; *n* is in parentheses.

Treatments	Mature seeds per capsule (%)				Mature seeds per flower (no.)			
----- 1991 -----								
1	72.5 \pm 25.2	(16)	A ^a		124.3 \pm 155.8	(32)	A	B
2	69.9 \pm 27.5	(12)	A		189.6 \pm 91.6	(12)	A	
3	22.5 \pm 23.6	(11)		B	20.4 \pm 49.5	(34)		B
4	49.3 \pm 34.0	(7)	A	B	105.6 \pm 130.0	(9)	A	B
----- 1992 -----								
1	58.5 \pm 27.5	(6)	A	B	93.8 \pm 94.7	(8)	A	B
2	90.5 \pm 5.0	(10)	A		156.5 \pm 35.3	(10)	A	
3	45.9 \pm 24.8	(7)		B	46.0 \pm 42.5	(10)		B

^aBonferroni *t* tests comparing treatments within each year. Means with same letter are not significantly different ($P < .05$).

were low. When aborted fruits were eliminated from the analysis in 1991 (50%), more mature seeds were produced per flower in 1991 than in 1992. This also suggests that the larger number of bees present in 1991 increased the numbers of seeds produced in plants with sufficient moisture to produce mature fruits. Fruit initiation may be pollinator limited, but mature fruit and seed production are primarily limited by resources such as water (Galen and Newport 1988, Horvitz and Schemske 1988, Ashman and Stanton 1991).

It is not known whether the rarity of bees observed in 1992 could be related to drought conditions or snow and cold weather in late June. Many species of bees were seen foraging on other flower species in Little Valley during May 1992 (personal observation). Numerous male *Bombus vosnesenskii* were observed foraging on several flower species on the study site during July, but few females of any *Bombus* species were seen during the *G. newberryi* flowering period. In contrast, an open flower in 1991 could rarely be found with pollen remaining on the anthers. Throughout 1992, most open *G. newberryi* flowers had nectar and abundant pollen available as potential pollinator rewards.

There were large populations of *Lupinus sellulus* adjacent to patches of *G. newberryi*, and Aster species and *Perideridia bolanderi* (Gray) Nels. & Macbr. were common from July through September. In 1991 *Bombus edwardsii*, *B. fervidus*, and *B. appositus* were seen visiting only *G. newberryi*. *Bombus vosnesenskii* was usually observed visiting *L. sellulus* with

occasional visits to several *G. newberryi*. In 1992 the few bees observed visited a variety of flowers, and none showed a preference for *G. newberryi*. We observed a few nectar-robbing visits from outside the flower by male *B. vosnesenskii* in 1992.

Ultraviolet markings in the center of the corolla and on the outside of petals attract and guide bees to nectar sources (Silberglied 1979, Kevan 1983, Waddington 1983, Waser 1983b). Bumblebees were often observed flying quickly and directly in a straight line from *G. newberryi* flower to flower. When entering a flower, a nectar-foraging bee positions its ventral surface over the anthers in the staminate phase and over the stigma in the pistillate phase. Bees were rarely observed collecting *G. newberryi* pollen.

There was no difference in the rate of seed germination between self- and cross-pollinated flowers. Seed production is not affected by type of pollination, but it may be limited anatomically in unvisited self-pollinated flowers. As the flower closes, the stigma bends over and touches only one or two of the anthers. Caged plants that were hand-pollinated with pollen from a flower on the same plant produced as many seeds as open plants or plants with supplemental hand cross-pollination.

Plants in wetter soil had larger, showier flowers than those in dry soil. Pollinators are usually attracted to larger flowers (Galen and Newport 1988, Ashman and Stanton 1991). In 1991 the surface soil was very dry in a large part (1800 m²) of the study site. Fewer seeds matured per flower and more seed capsules

aborted in the dry area, suggesting that inadequate soil water can limit the number of seeds produced per flower. Surface soil throughout the study site appeared wetter in 1992. The positive relationship between soil water at flower opening and number of mature seeds produced in 1992 indicates the importance of sufficient water resources in determining seed set.

Facultative self-compatibility allows *G. newberryi* to produce seeds even when pollinators are rare. Vegetative reproduction requires less energy (Waller 1988) and may be used in addition to or in place of flower production or sexual reproduction. Of 10 plants that were dug up, only one did not have an attached lateral rhizome. Since data will continue to be collected from this site, we did not dig up a sufficient number of plants to be able to determine size of clones or average number of rhizomes per ramet.

There was no significant difference in population size, number of flowers, or mean number of seeds produced per flower between 1991 and 1992. Some plants marked in 1991 that remained covered with 1 cm of water or more from the natural creek diversion did not survive.

Larger *G. newberryi* flowers are found in wetter areas and produce more mature seeds than flowers in drier soil areas. There was a significant relationship between number of pollinators present and number of seeds produced only when pollinators are rare. There was no difference in seed production between flowers with xenogamous and geitonogamous pollination. Facultative self-compatibility and vegetative reproduction allow plants to produce seeds or ramets when pollinators are limiting. *Gentiana newberryi* appears well adapted to survive during unpredictable periods of pollinator availability and soil moisture.

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